FINAL REPORT FOR JOINT VENTURE PHASE 2
BETWEEN U.S. DEPARTMENT OF
AGRICULTURE, FOREST SERVICE ROCKY
MOUNTAIN RESEARCH STATION WORK
UNIT 4152 AND REGENTS OF THE
UNIVERSITY OF COLORADO

FINAL REPORT FOR JOINT VENTURE PHASE 2 BETWEEN U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE ROCKY MOUNTAIN RESEARCH STATION WORK UNIT 4152 AND REGENTS OF THE UNIVERITY OF COLORADO

FOREST SERVICE AGREEMENT: 00-JV-11221605-221

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PROJECT TITLE: The effects of multiple predators on ponderosa pine canopy herbivores and dwarf mistletoe demography.

SYNOPSIS

This document is the final report of Phase 2 for Joint Venture 00-JV-11221605-221 between the USDA Forest Service Work Unit 4152 and the Regents of the University of Colorado. We begin this Final Report by reviewing the biology of the system in which we work and the theoretical questions we are addressing. We then provide a summary of the work completed during Phase 2 and compare this completed work to the tasks outlined in the work plan provided in the Phase 1 Final Report submitted to the Forest Service on June 1, 2001. We have accomplished nearly all the tasks outlined in the Work Plan. In two instances, we decided to continue experiments originally planned to end in August 2001 until August of 2002. Because these experiments are on going, the completion of certain tasks was postponed.

A. INTRODUCTION

Ponderosa pine (*Pinus ponderosa*) has the largest geographic range of any conifer in North America (Baumgartner and Lotan 1988). Ponderosa pine ecosystems dominate much of the montane West, and are of tremendous ecological and economic importance. Parasites and herbivores pose formidable challenges to plant fitness generally (e.g. Howe and Westley 1998; Fritz and Simms 1992), and to ponderosa pine specifically (Furniss and Carolin 1977; Baumgartner and Lotan 1988; Hawksworth and Wiens 1996). Innate resistance represents one important line of defense against such natural enemies (Howe and Westley 1988; Fritz and Simms 1992). A second and perhaps equally important source of protection is provided by those predators that keep such natural enemies in check according to the adage that "the enemy of my enemy is my friend" (Hairston et al. 1960). The goal of the research for this Joint Venture has been to investigate the effects of predators on ponderosa pine herbivores and to investigate how parasite-induced changes in ponderosa pine morphology affects the assemblage of arthropod predators residing in pine canopies.

The efficacy of predators as protectors of plants likely depends on many factors, the most important of which may be the composition of the predator assemblage. Predator assemblages vary in the protection they provide plants from herbivores because individual predator taxa can vary in effect strength. In addition, interactions *among* multiple predators in an assemblage can change their combined effect strength such that as an assemblage, predation strength may be greater or less than the sum of the predator's

individual effects (Sih et al. 1998).

We are conducting two separate lines of inquiry investigating predator assemblages in ponderosa pine forests. Southwestern dwarf mistletoe (*Arceuthobium vaginatum* ssp. *cryptpodum* (Engelm.) Hawksw. & Wiens) is an important parasite of ponderosa pine throughout the Intermountain West. This dwarf mistletoe can cause radical changes in pine morphology, including branching pattern, branch shape and needle length (Hawksworth and Wiens 1996), and colloquially such misshapen, parasitized branches have been referred to as "brooms" or "witch's brooms". We hypothesized that such changes in pine branch structure likely affect the canopy arthropod community, including the assemblage of arthropod predators.

Our second line of inquiry investigates the role of birds and ants in the community ecology of pine canopies. Birds (Askenmo et al. 1977; Otvos 1978; Gunnarsson 1983; Hogstad 1984; Riechert and Hedrick 1990; Wise 1993; Marquis and Whelan 1994) and ants (Petal 1969; Kajak et al. 1972; Howard and Oliver 1978; Haemig 1992; Wise 1993; Aho et al. 1997; Halaj et al. 1997) have long been recognized as effective predators of arthropods in many ecosystems, including coniferous tree canopies. There is also some evidence that bird and ant predation of herbivores can provide benefit to forest trees (Skinner and Whittaker 1981; Fowler and Macgarvin 1985; Warrington and Whittaker 1985; Mahdi and Whittaker 1993; Marquis and Whelan 1994). While the individual effects these predators directly on arthropods and indirectly on trees has received attention, no work to-date has investigated whether the interactions between birds and ants changes the net effect of this predator assemblage.

B. THE FIELD SITE AND EXPERIMENTAL SYSTEM
Field site

This work is being conducted at the Manitou Experimental Forest, an administrative unit of the USDA Forest Service Rocky Mountain Experiment Station. This site, located in Woodland Park, Colorado (39'00 N, 105'19 W), occupies 6730 ha, and our work was conducted at an elevation of 2400 m.

Dwarf mistletoe

Southwestern dwarf mistletoe is a common parasite of ponderosa pine (*Pinus ponderosa* var. *scopulorum* Laws.) in these forests. Where parasitism is severe, pine morphology is radically altered (Hawksworth and Wiens 1996) and branches often take a broomed shape. The stands where our work on dwarf mistletoe is conducted are approximately composed of a single cohort of 70 years pines of approximately 10 m in height.

Predators: Ants and birds

The gravel-dome mounds of *Formica fusca* L. (Greg 1963) occur near the bases of ponderosa pines in this forest at a density that sometimes exceeds 125 per hectare (Mooney unpublished data), and in these areas *F. fusca* is the only ant found on ponderosa pine (Mooney pers. ob). The guild of foliage-gleaning birds at Manitou is dominated by Mountain chickadees (*Parus gambeli*) and nuthatches (*Sitta carolinensis, S. pygmaea, and S. canadensis*).

A review of dietary literature reveals that chickadee (*Parus* spp.) and nuthatch (*Sitta* spp.) prey are composed principally of lepidopterans, followed closely by flying hymenopterans, and coleopterans, and more distantly by spiders, psocopterans, homopteras, and others (Dahlsten and Copper 1979; Grundel and Dahlsten 1991;

Pravosudov et al. 1996; Block and Finch 1997). There is little evidence to suggest that these birds prey on formicid ants to a significant degree, despite ample opportunity (Dahlsten and Copper 1979; Pravosudov et al. 1996; Mooney pers. ob.). *Formica fusca* feed on nearly all orders of arthropods commonly found in pine canopies, i.e. they have a prey base very similar to that of the birds (Mooney unpublished data). While these birds and ants may not interact as predator and prey, there is evidence from studies on their congeners of bi-directional interference competition, i.e. birds interfere with ant foraging (Haemig 1997), and ants interfere with bird foraging (Haemig 1992, 1994, 1999). This predator–predator interaction makes it likely that the combined effects of bird and ant predation will be less than that predicted based on the two individual effects (Sih et al. 1998).

While birds and ants are effective predators of some arthropod herbivores, *F. fusca*, like many ants (Holldobler and Wilson 1990), commonly displays aggressive defense of some homopterans so as to guarantee their access to honey dew (so-called "tending") (Mooney pers. ob.). *Cinara* spp. (Homoptera: Aphididae) are abundant in pine canopies, and *F. fusca* opportunistically tend these aphids (Mooney, pers. ob.). This mutualism adds a level of complexity to the canopy community in that ants have a positive effect on those herbivores they tend.

C. EFFECT OF DWARF MISTLETOE ON CANOPY ARTHROPOD COMMUNITY
Introduction.

The purpose of this work was to document the effects of dwarf mistletoe on the pine canopy arthropods. The prediction was that branches parasitized by dwarf mistletoe will have significantly different arthropod communities than non-parasitized branches because of differences in the two branch morphologies.

Methods.

Two separate projects were designed to approach these questions. First, we collected arthropods from parasitized and unparasitized branches to look for correlative patterns in community structure (the "Correlative Experiment"). Second, we performed a manipulative experiment to identify the mechanism behind differences in these two arthropod communities (the "Manipulative Experiment").

Correlative Experiment

We selected 10 pairs of parasitized and non-parasitized branches ranging in length from 1.4 m to 2.0 m in length. All pairs were selected within a 3 ha section of Manitou with high rates of dwarf mistletoe parasitism. Branches within pairs were selected from separate, but neighboring trees. Branches were specifically selected to be of similar size so that the distinction between parasitized and branches was not confounded with other morphological variables. We have noticed that the morphology of parasitized branches leads to an accumulation of needles. To determine whether such accumulations affect branch arthropod communities we removed the dead needles accumulated on each branch, collected and preserved the arthropods associated with those needles, and later weighed them in the laboratory. Next, we collected and preserved arthropods from all branches by beating them over drop cloths in a standardized fashion. All arthropods were preserved in 75% ethanol. We then recorded branch length, width, height, diameter, and compass bearing (i.e. which side of the tree the branch was on), total branch mass, foliage-free mass, foliage mass, and branch age. We also counted the number of "branch crosses" or points where two branchlets touched each-other within each branch.

Parasitized branches generally have a less linear and more twisted morphology, and this measure quantifies this to a certain extent.

For each branch we made separate collections of arthropods from dead needles and from the remainder of the branch (i.e. 2 samples per branch). This project thus generated a total of 40 arthropod samples (i.e. 10 pairs x 2 branches/pair x 2 arthropod collections / branch = 40 samples). In most cases we sorted arthropods to order, but in some cases to genus. Distinctions between immature and mature life stages were also made in some cases. The list of taxonomic categories is as follows: *Cinara* spp. (Aphididae: Homoptera), *Essigella* (Aphididae: Homoptera), other Homoptera, Hemiptera nymph, Hemiptera adult, Coleoptera larva, Coleoptera adult, Lepidoptera larvae, *Formica* spp. (Formicidae: Hymenoptera), Psocoptera, Neuroptera, Thysanoptera, Collembola, Pseudoscorpiones, and Araneae. Each arthropod was identified to one of these categories and then measured to the nearest millimeter.

We performed two statistical tests to identify differences between arthropods from parasitized and unparasitized branches. Body size distributions of arthropods were analyzed by regressing log-transformed mean abundance (n=10) on body size length classes ranging from 1.0 mm to 14.0 mm in 1.0 mm increments. This transformation linearized the two observed size distribution, and the coefficients of determinations were high in both cases ($R^2=.89$ for unparasitized, $R^2=.92$ for parasitized). The two body size distributions were then compared using the regression coefficients because these coefficients represent the distribution parameters.

Overall differences in taxonomic composition were analyzed using MANOVA (Johnson1998), where the abundance of each arthropod taxa per kilogram of branch mass was treated as a separate dependent variable. Because of accumulation of type II error (i.e. the likelihood of false positives), it is generally not recommended to perform individual ANOVAs in a one-variable-at-a-time fashion (Johnson 1998). Instead we inspected the mean abundance of each taxonomic category from parasitized and unparasitized branches in order to qualitatively estimate which taxa might be responsible for any community-level differences indicated by a significant MANOVA.

Manipulative Experiment

We hypothesized that differences between arthropod communities on parasitized and unparasitized branches are likely due to the more complex branching pattern of parasitized branches and that this branching pattern traps dead needles falling from the canopy. Unparasitized branches do not accumulate significant quantities of dead needles. To test this hypothesis we constructed 18 "artificial parasitized branches" by attaching dead branch material to a living, unparasitized branch with wire, and then stocking this branch with approximately 1 kg of dead needles. Each of these artificial parasitized branch was paired with (1) a nearby parasitized branch and (2) an unmanipulated branch without dwarf mistletoe.

Installation of this design was completed by late June, 2001. In order to provide time for differences in arthropod communities to develop we will not disturb these branches until August of 2002.

We will use a again perform a MANOVA to test for differences between branches with artificial parasitism, parasitism, and no parasitism. Any significant differences between artificially parasitized and unparasitized branches can be ascribed to our manipulations. We can then test whether such the artificially parasitized branches branches are significantly different from parasitized branches.

Results.

Correlative Experiment

Mean morphological measurements for parasitized and non-parasitized branches are listed in Table 1. There were not statistically significant differences among parasitized and non-parasitized branches except in the number of crosses (P<0.0001) and mass of dead needles held by branches (P=0.003).

The arthropod size distributions of parasitized and unparasitized branches were very similar (Fig. 1). The intercepts were nearly identical (2.90 for unparasitized and 2.89 for parasitized) indicating that overall arthropod abundance are similar. The slopes of both distributions were negative, and although the slope for unparasitized branches was steeper than parasitized, this difference was not significant (P=0.76).

All MANOVA test statistics (Wilk's Lambda, Pillai's Trace, Hotelling–Lawley Trace, Roy's Greatest Root) suggested a community-level difference in taxonomic composition of parasitized and unparasitized branches (P=0.0204). An inspection of mean taxonomic abundance indicate that the differences are due to lower abundance of aphids (*Cinara* spp. and *Essigella* spp.) and Collembola and increases in spiders (Araneae), Hemiptera, and Psocoptera on parasitized branches as compared to unparasitized branches (Fig 2).

Table 1. Parasitized and unparasitized branch morphological measurements and ANOVA results testing for differences between the two branch types.

measurements	non-parasitized branches mean (SD)	parasitized branches mean (SD)	test for differences between branch types F1,19	P
length (m)	1.92 (0.33)	1.69 (0.24	3.32	0.085
width (m)	1.63 (0.75)	1.54 (0.32)	0.12	0.7333
height (m)	1.13 (0.30)	1.07 (0.26)	0.22	0.6427
diameter (mm)	54.0 (6.7)	59.0 (8.9)	2.02	0.1726
crosses (#)	0.00 (0.00)	6.3 (2.4)	68.56	<0.0001
bare mass (g)	2678 (1398)	3785 (1693)	2.54	0.1281
foliage mass (g)	2344 (1870)	1720 (894)	0.91	0.3535
total mass (g)	5002 (2718)	5505 (2514)	0.17	0.6845
branch age (yr)	26 (11.8)	34.5 (8.8)	3.35	0.0838
needles (g)	4.60 (14.45)	159.84 (142.2)	11.8	0.003

Manipulative Experiment

The manipulative experiment has been installed, but arthropods will not be collected from these branches until August, 2002.

Discussion.

Although branches did not differ significantly in most morphological categories, correlative data suggested there was a significant overall difference in arthropod community composition between parasitized and unparasitized branches. Parasitized branches supported fewer aphids that feed on phloem sap and more psocopterans that are detritivores. It appears that parasitism by dwarf mistletoe may change the trophic structure of pine branches from one based on consumption of pine primary production to one based on a detritivore pathway. The fact that spider abundance was higher on parasitized branches provides evidence of differences in the third trophic level of this

system. Whether these differences are due to bottom-up influences (i.e. changes in the herbivore community) or due to differences in top-down influences of predators such as birds is unclear. The fact that the size distributions of arthropods on parasitized and unparasitized branches were so similar suggests that there may not be a difference in top–down pressures, possibly making the bottom–up explanation more likely.

Comparison of accomplishments with Work Plan tasks.
Task 1. "Complete the identification and processing of the arthropod samples."

Accomplished.

Task 2. "Perform statistical analyses on these data, as described above."

Accomplished.

Task 3. "Report results in the form of publication and/or oral presentation."

These results will be published with results from the Manipulative Experiment.

Task 4. "Establish manipulative field experiment investigating the mechanisms of dwarf mistletoe effects on canopy arthropod communities."

Accomplished.

Task 5. "At the conclusion of the summer we will collect the arthropods from all branches" [from the Manipulative Experiment].

A decision was made to allow the manipulative experiment to run for an additional season. As a result, arthropods from this work will be collected in August of 2002, and analyses of these data will progress at that point.

Task 6. "Identify all arthropods from Task 5 above."

This will be done following arthropod collection in August 2002.

Task 7. "Perform statistical analyses."

This will be done following arthropod collection in August 2002.

Task 8. "Report results in form of publication and/or oral presentation."

This will be done following arthropod collection in August 2002. Results from Manipulative Experiment and Correlative Experiment will be published together.
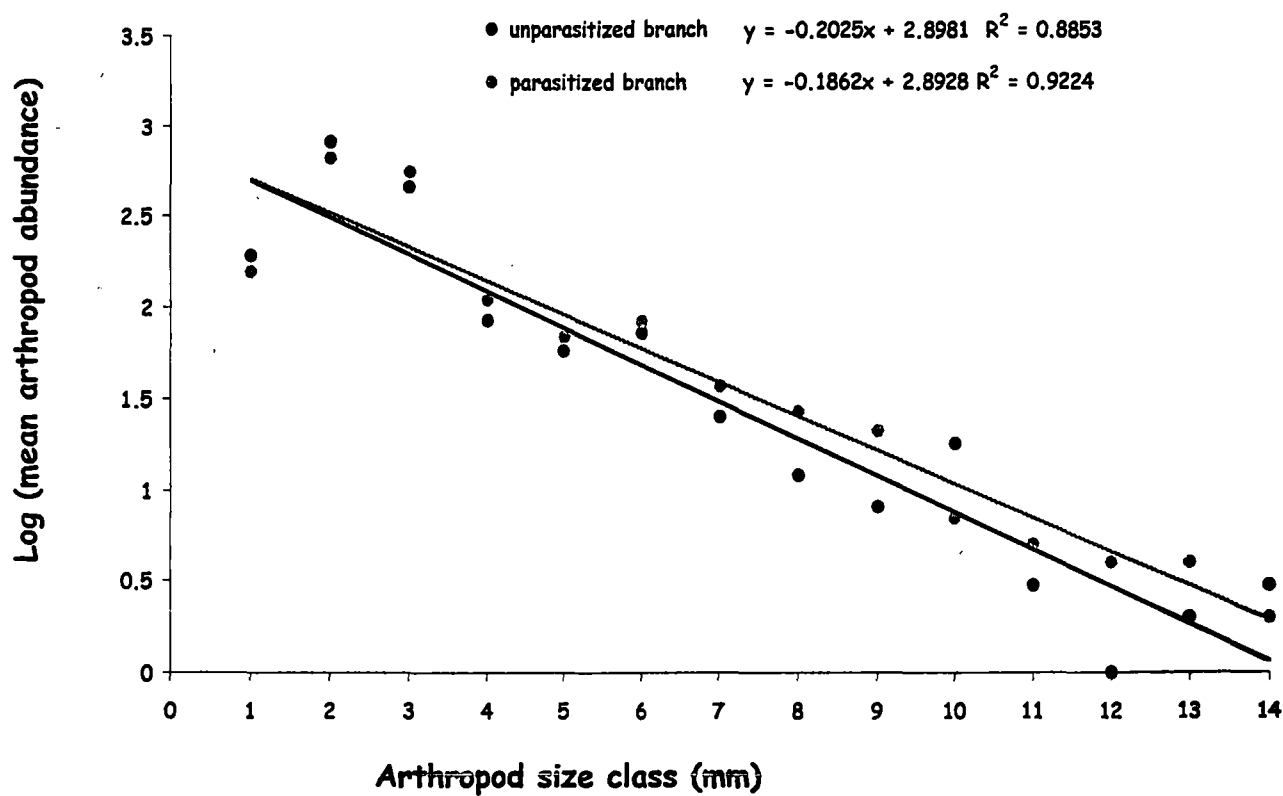
Fig. 1: Arthropod size distributions for parasitized and unparasitized branches. Mean abundance (N=10) for each branch type in each size class was log transformed. The slopes and intercepts for the two distributions are not significantly different. See text for details.
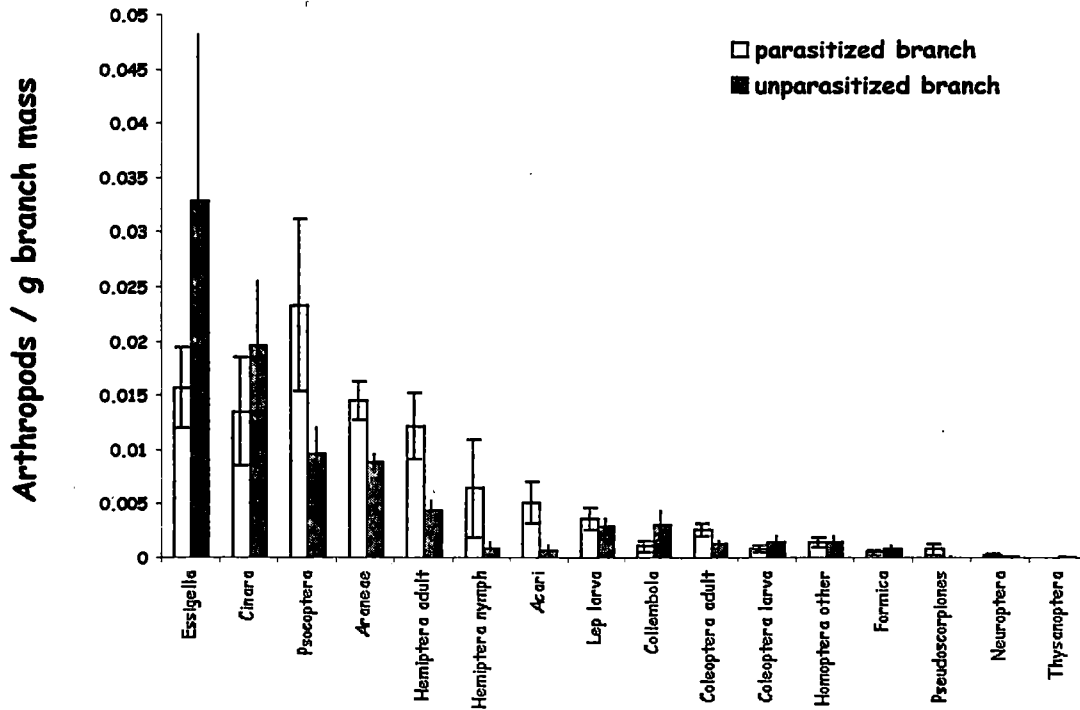
Fig.2: Abundance (# / g branch mass) of sixteen arthropod taxonomic groupings (± 1 SE) from branches parasitized by dwarf mistletoe (n=10) and unparasitized (n=10).

D. EFFECTS OF BIRDS AND ANTS ON CANOPY ARTHROPOD COMMUNITY

Introduction

The purpose of this experiment was to determine the effects of bird and ant predation on the ponderosa pine canopy arthropod community. We continued work on two separate, previously established long-term projects, a factorial experiment of bird and ant exclusion (the "Bird and Ant Exclusion Experiment") and a whole-tree bird exclusion experiment (the "Whole Tree Bird Exclusion Experiment").

Methods.

Bird and Ant Exclusion Experiment

In June of 2000, prior to the period covered by Phase 2 of this Joint Venture, we initiated a factorial experiment of bird and ant exclusion in ponderosa pine canopies (Fig. 3). We selected 16 pairs of trees closely associated with identified mounds of *F. fusca*. We manipulated one tree from each pair with an ant exclusion treatment (a sticky barrier around tree bases), selected pairs of branches on both trees, and then manipulated one branch from each pair with a bird-exclosure (2.5 cm-opening mesh bags). These treatments generated a split-plot design with bird manipulation set within ant manipulation. This design created branches in each of the following four treatments: ant-exclusion, bird-exclusion, ant and bird exclusion, and controls. We collected arthropods from all branches by beating them over drop cloths in a standardized fashion and preserving them in 75% ethanol. We made these collections in early August and mid-September. All arthropods were sorted at least to the taxonomic level of order, in some cases family (e.g. lepidopteran larvae), and we identified aphids (Aphididae: Homoptera) to the generic level. For every arthropod we also recorded its size to the nearest millimeter. Figure 4 shows a sample arthropod sorting form.

We adjusted the design of this experiment in June 2001. We added two additional trees to each existing pair and switched from the split-plot design (Fig. 3) to a one-treatment-per-tree scenario, i.e. a two-by-two factorial design (Fig. 5a). In addition, we increased the sample size for this experiment from 16 branches per experimental treatment to 21 branches, and we collected arthropods in June, July, August, and September. We began processing of arthropod samples according to the same protocol as was just described in the preceding paragraph.

Whole Tree Bird Exclusion Experiment

In July 1999 we constructed 16 whole-tree bird exclosures around 2–3 m tall trees, and paired each bird exclosure tree with a nearby control. We have collected data on levels of foliage herbivory and arthropod abundance each year. In June of 2001 we collected data on levels of foliage herbivory on all trees. We randomly selected 40 one-year-old and 40 two-year-old needles from each tree and recorded the area of each needle damaged by herbivores. We analyzed these data using a repeated-measures ANOVA and tested for effects of year (2000, 2001), needle age (one- or two-year-old), and treatment (bird exclosure or control).

Between June and September we collected data on arthropod abundance on control and bird exclusion trees. On five occasions we performed 12 minute visual searches of the canopy of each tree and recorded the identity of all arthropods seen during this period. Exclosures were also checked and repaired as needed.
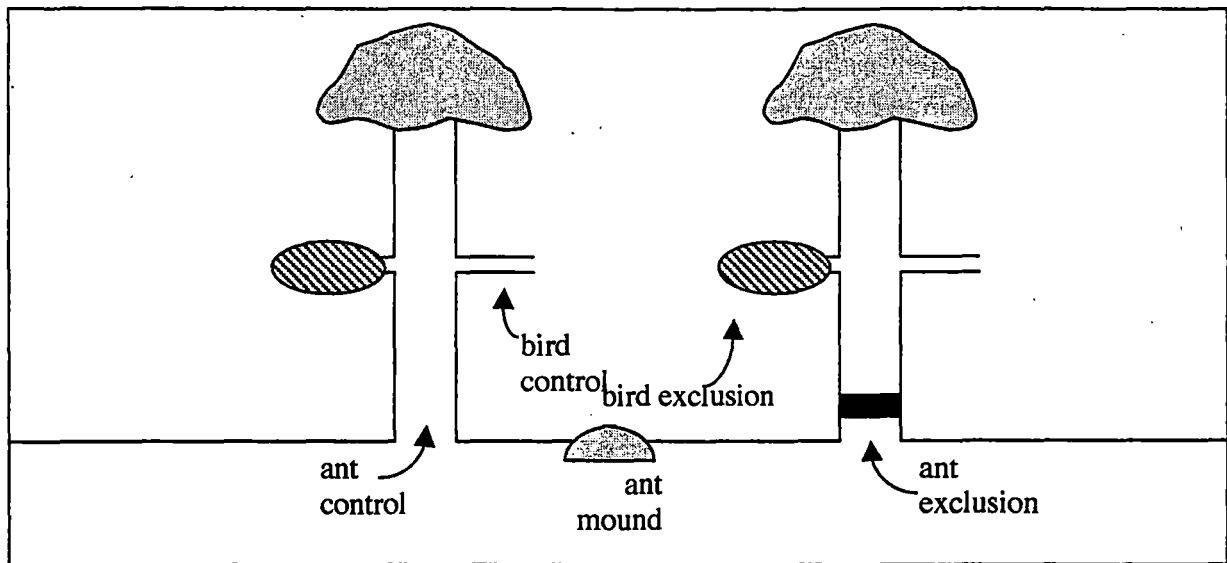
Fig. 3: 2000 Experimental design to test for individual and combined effects of bird
and ant predation directly on ponderosa pine arthropods.

Sample: 8AC - 8/11	Date Sorted: 3/5/2001			By: Jan Halah		
Vials: unknown [ ]; Araneae [x]; other [x]; photo [ ]: [ ] Time:						
50cc: Y/N	0-1mm	1-2mm	2-3mm	3-4mm	4-5mm	>5mm	Total

	0-1mm	1-2mm	2-3mm	3-4mm	4-5mm	>5mm	Total
Aphididae Cinara	528 12	50 27 50 37 531 1 161	9				182
Aphididae Essigella [ ]	4	50 12	74				
Homoptera (other)							
Araneae	1 1	6 111 9	2 2				12
Acari	51						
Hemiptera (nymph)							
Hemiptera (adult)				2	1		
Coleoptera adult B=blk, G=gold							
Coleoptera larva		1	1	1	1		
Lepidoptera larva G=Geometridae					1 1	6 1	2
Formica sp.	1						
Hymenoptera (other)							
Psocoptera			1				
Pseudoscorpiones							
Neuroptera		2					
Thysanoptera		1					
Collembola		11					
Diptera	1	1					
Unknown (no wing)							
Unknown (wing)							
Total							

#s are single digit unless circled; #s in ">5mm" category are the sizes not #s of individuals; # in box = winged, otherwise wingless; sub-types within rows (indicated in column 1) denoted by LETTER=#
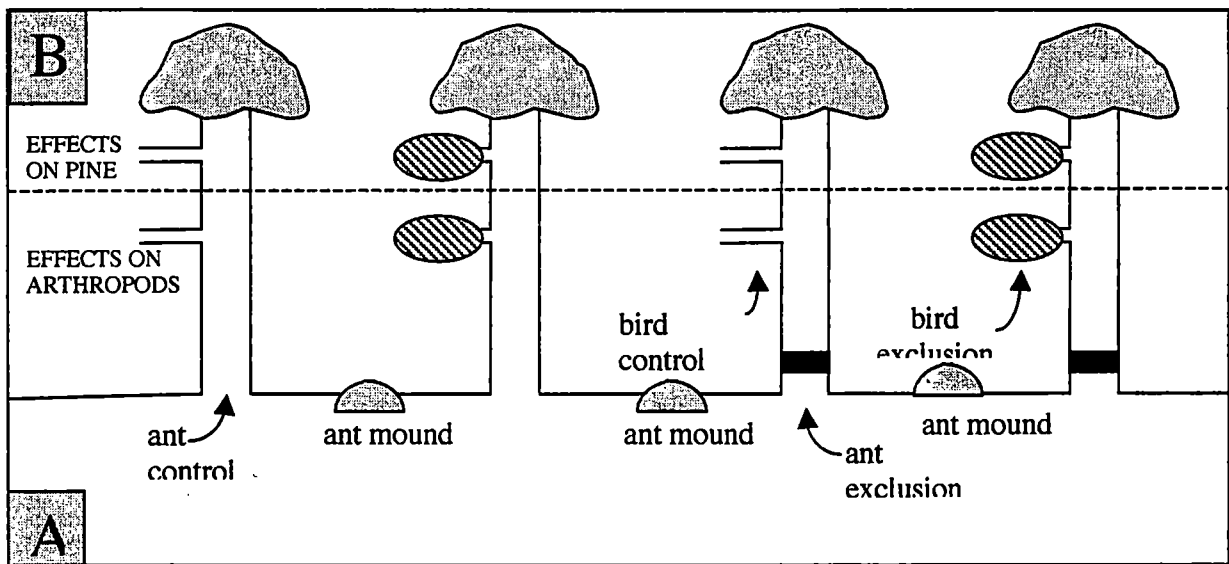
Fig. 5: 2001 Experimental design to test for individual and combined effects of bird and ant predation (A) directly on ponderosa pine arthropods and (B) indirectly on ponderosa pine itself.

Results.

Bird and Ant Exclusion Experiment

Analyses of arthropod data from the summer of 2000 were provided in the Phase 1 Final Report. In June 2001 we adjusted the experimental design from the original split-plot design (Fig. 3) to a factorial design (Fig. 5a), sample size was increased from 16 to 21 blocks (i.e. 84 trees). We collected arthropods in June, July, August and September. We have processed the June samples to-date but have not analyzed these data.

Whole Tree Bird Exclusion Experiment

We successfully collected all arthropod and herbivory data and maintained the integrity of the bird exclosures. We have not, as yet, analyzed the arthropod data. Our analysis of the herbivory data (Fig. 6) showed an overall significant effect of bird exclosure on rates of herbivory (P=0.03), a significant effect of year (P=0.0001) and a significant effect of needle age (P=0.0006). Two-way interactions between year, needle age, and treatment were not significant, although the three-way interaction was marginally significant (P=0.076).

Discussion.

Bird and Ant Exclusion Experiment

The redsign of the experimental and collection of arthropod were successful.

Whole Tree Bird Exclusion Experiment

All data were collected successfully. We have not, as yet, analyzed the arthropod data from this experiment. The herbivory data demonstrates that rates predation by birds has important consequences for ponderosa pine by changing rates of foliage herbivory. This effect is stronger for two-year-old than one-year-old needles. Although the amount of herbivory varied between years, the strength of the top-down effect of birds did not.

Comparison of accomplishments with Work Plan tasks.

Task 1. "We will continue our work investigating the effects of birds and ants [, i.e. the Bird and Ant Exclusion Experiment,] on the pine canopy arthropod community with one significant change. Our 2000 our design was a split-plot where the bird treatment was nested within the ant treatment ... We will add two additional trees to each existing pair and switch from the current tree-pair design to a one-treatment-per-tree scenario. In addition, we will increase the sample size for this experiment from 16 branches per experimental treatment to 20 branches, and we will sample four times during the summer of 2001."

Accomplished.

Task 2. "In 1999 16 whole-tree bird exclosures [,i.e. from the Whole Tree Bird Exclosure Experiment,] were constructed, and each tree was paired with a nearby control. This summer ... we will perform visual surveys (1 per month = 4) of pine arthropod fauna on these trees. In addition, early in the field season we will collect foliage herbivory data from needles flushed in 2000. We will also repair and maintain these bird exclosures as needed."
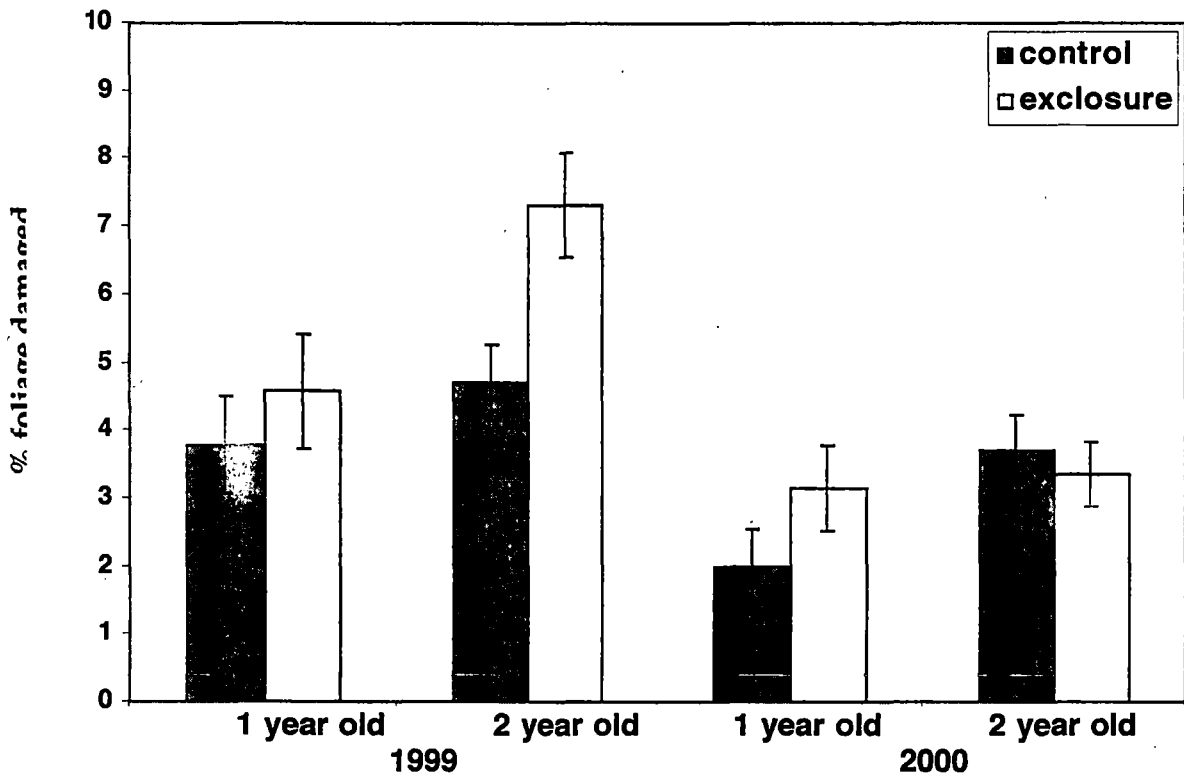
Fig. 6: Rates of herbivory (± 1SE) of 1 year old and 2 year old ponderosa pine foliage from bird exclosure and control trees in 1999 and 2000. Effects of experimental treatment, foliage age, and year were all significant, but there were no significant two- or three-way interactions. See text for details.

Accomplished.

E. EFFECTS OF ANTS ON AVIAN FORAGING

Introduction.

This experiment was conducted during the summer of 2000. The goal of this experiment was to determine whether ants affect the behavior of canopy foraging birds. This work is an important companion experiment to our work investigating the effects of birds and ants on canopy arthropods as it begins to elucidates the pair-wise interactions between the two predators –birds and ants – in this system.

Results from this work were presented in the Phase 1 Final Report submitted to the Forest Service on June 1, 2001. Our findings were presented at the Annual Meeting of the Guild of Rocky Mountain Population Biologists on September 22, 2001 in Abiquiu, New Mexico, and at the Annual Meeting of the Ecological Society of America on August 7, 2001 in Madison, Wisconsin. See Appendix for abstracts.

Comparison of accomplishments with Work Plan tasks.
Task 1. "Report results in form of publication and/or oral presentation."

Accomplished. See Appendix for abstracts.

F. EFFECTS OF WINTER BIRD PREDATION ON CANOPY ARTHROPODS

Introduction.

Many spiders over-winter as juveniles (Gunnarsson 1983; Gunnarsson and Hake 1999; Wise 1993; Foelix 1996), and past studies of coniferous forest systems have found that winter predation by birds significantly reduces spider abundance (Gunnarsson 1983; Gunnarsson and Hake 1999). The purpose of this experiment was to determine whether winter resident birds in ponderosa pine forests (*Parus* spp. and *Sitta* spp.) have similar effects.

Results from this work were presented in the Phase 1 Final Report submitted to the Forest Service on June 1, 2001. Our findings from this work were presented at the Annual Meeting of the Guild of Rocky Mountain Population Biologists on September 22, 2001 in Abiquiu, New Mexico. See Appendix for abstracts.

Comparison of accomplishments with Work Plan tasks..
Task 1. "Report results in form of publication and/or oral presentation."

Accomplished. See Appendix for abstracts.

G. INDIRECT EFFECTS OF PREDATORS ON PONDEROSA PINE

Introduction.

This was a new project to begin in Phase 2 of this Joint Venture. The purpose of this work was to determine the individual and combined <u>indirect effects</u> of birds and ants on ponderosa pine. This work is closely related to Section D described above, which characterized the <u>direct effects</u> of birds and ants on the ponderosa pine canopy arthropod community.

Methods.

In order to determine whether the exclusion of birds and ants from ponderosa pine has indirect effect on the pine itself, we selected an additional branch from each tree in the <u>Bird and Ant Exclusion Experiment</u> (see section D above; Fig 5a,b). While arthropods are being collected from some branches on these trees (see Section D; Fig. 5a), these new branches (Fig. 5b) will not be disturbed for the duration of the experiment. At the conclusion of the experiment (August 2002) we will measure growth rates and rates of herbivory. These data will allow us to test for whether there are indirect effects of birds and ants on ponderosa pine, and to compare the combined indirect effects of these two predators with their individual indirect effects.

Results.

A separate branch was selected and tagged on each of the 84 trees from the <u>Bird and Ant Exclusion Experiment</u> (Fig 5b).

Discussion.

Originally we had planned to conclude this experiment in September 2001. A decision was made to continue this work through the summer of 2002. Because this experiment is still ongoing, we did not disturb these branches. Data on branch growth and rates of herbivory will be collected, as planned, when this experiment concludes.

Comparison of accomplishments with Work Plan tasks.

Task 1. "Select an additional experimental branch on all experimental trees. These branches will not be disturbed for the duration of the experiment."

Accomplished

Task 2. "At the conclusion of the 2001 season we will measure needle herbivory, needle length, needle density, branch elongation (primary growth) and branch increment increase (secondary growth)."

These data will be collected at the conclusion of this experiment in 2002.

Task 3. "Statistically analyze these data to test for indirect effects of predator manipulations on ponderosa pine."

This analysis will proceed following data collection in 2002.

Task 4. "Report results in form of publication and/or oral presentation."

These results will be reported following data collection and analysis in 2002.

H. EFFECTS OF BIRDS ON ANTS

Introduction.

The purpose of this work is to investigate the mechanisms by which birds affect ants. Ants have been shown to jump from trees to escape birds (Haemig 1992; personal observation), and it is our prediction that differences in ant abundance between bird

exclusion and control branches may be due not to predation, but to an increase in such escape behavior.

Methods.

We suspended 10 50 cm x 75 cm sticky traps approximately 50 cm beneath branches with bird-excluding netting and 10 beneath control branches for 48 hours in early July. During that time we counted the number of ants visiting each branch for two separate 10 minute periods. At the conclusion of the 48 hour period we collected the sticky traps and counted the number of ants per trap.

To test for a difference in sticky-trap capture rate of ants between bird exclosure and control branches we an ANCOVA with ant visitation rate as a covariate. If there is a correlation between the number of ants visiting each branch and the number caught on the corresponding sticky trap an ANCOVA would allow us to determine whether there are differences in ant jumping rate between treatments, corrected for ant abundance on each branch. In the absence of a correlation between ant visitation and trapping rates, a simple one-way ANOVA is the appropriate test for differences in trapping rate between control and bird-exclusion branches.

Results.

There was no linear association between number of ants counted visiting each branch and the number of ants caught on the sticky trap beneath the same branch (P=0.56). Without this linear association, an ANCOVA was inappropriate so we performed a simple one-way ANOVA. A mean of 15.1 $\pm$ 5 ($\pm$ 1 SE) ants were caught from control branches and 16.1 $\pm$ 6 ($\pm$ SE) from bird exclusion branches, and this difference was not significant (P=0.85).

Discussion.

These results suggest that rates of ant jumping from experimental branches are not affected by birds. This finding was surprising to us for for several reasons. First, other studies investigating bird–ant interactions have demonstrated this behavior with congeners of the species with which we work (Haemig 1992). Second, we have data showing that birds reduce ant abundance (see Final Report Phase 1), but dietary studies suggest Chickadees and Nuthatches do not feed on formicid ants (see Section B above). We hypothesized that the reduction in ant abundance was due to this jumping behavior. These results suggest that other another, as yet untested mechanism must be responsible for this treatment effect.

Comparison of accomplishments with Work Plan tasks.

Task 1. "Over the course of the summer we will count the number of ants going to and from bird exclosure and control branches and then put out the sticky traps."

Accomplished.

Task 2. "[W]e will ...count the number of ants caught per 48 hour period."

Accomplished.

Task 3. "We will test for a difference in sticky trap capture rate of ants between bird exclosure and control branches..."

Accomplished.

Task 4. "Report results in form of publication and/or oral presentation."

These results were presented at the annual meeting of the Ecological Society of America in on August 7, 2001 in Madison, Wisconsin. See Appendix for abstract.

I. DWARF MISTLETOE SEED COLLECTION
Introduction.
>This was a new project to begin in Phase 2. The purpose of this work was to gather seeds to be used by the Rocky Mountain Research Station in growth chamber experiments to begin in the fall of 2001.

Methods.
>*Arceuthobium vaginatum* and *A. americanum* are abundant at the Manitou Experimental Forest and near the University of Colorado in Boulder, Colorado respectively. We tracked the phenological progress of both species and upon fruit set brought multiple plants back to the laboratory and collected 1000 seeds of each.

Results.
>*Arceuthobium vaginatum* fruited in early August and *A. americanum* in late August. All fruits were ripe when collected, and we collected and stored in excess of 1000 seeds from each species.

Discussion.
>All seeds were collected.

Comparison of accomplishments with Work Plan tasks.
Task 1. "Collect approximately 1000 seeds from *Arceuthobium americanum* parasitizing lodgepole pine (*Pinus contorta*) and *A. vaginatum* parasitizing ponderosa pine (*P. ponderosa*)."

Accomplished.

J. CONCLUSION TO PHASE 2 FINAL REPORT
>Between June 1 and November 1, 2001, the period covered by Phase 2 of Joint Venture 00-JV-11221605-221, we initiated or maintained several large scale experiments investigating the effects of predators on ponderosa pine canopy ecology, and how parasitism by dwarf mistletoe affects the predator assemblage of pine canopies. The results from much of this work were presented at a major national meeting (the Ecological Society of America) and a regional meeting (Guild of Rocky Mountain Population Biologists). We accomplished nearly all of the tasks set forward in the Work Plan provided in the Phase 1 Final Report, with two notable exceptions. The

Manipulative Experiment of Section C was not completed because we judged that letting this experiment progress for an additional year would substantially increase the likelihood that this work will produce interesting and meaningful results. The Bird and Ant Exclusion Experiment of Section D will also be continued for an additional year for similar reason. While the extension of these experiments has meant that several of the outlined tasks for this work have not yet been accomplished, we believe that the benefit to postponing this work will be substantial.

LITERATURE CITED

Aho, T., M. Kuitunen, J. Suhonen, A. Jantti, T. Hakkari. 1997. Behavioral responses of Eurasian treecreepers , *Certhia familiaris*, to competition with ants. Animal Behaviour 54: 1283-1290.

Askenmo, C., von Bromssen, A., Ekman, J., and C. Jansson. 1977. Impact of some wintering birds on spider abundance in spruce. Oikos 28: 90-94.

Baumgartner, D.M. and Lotan, J.E. Eds. 1988. *Ponderosa Pine: The Species And Its Management.* Sym. Proc., Washington State Univ., Coop. Ext. Serv., Pullman.

Block, W.M. and D.M. Finch., Eds. 1997. *Songbird Ecology in Southwestern Ponderosa Pine Forests.* USDA Forest Service General Technical Report RM-GTR-292. 152 pp.

Dahlsten, D.L. and W.A. Copper, 1979. The use of nesting boxes to study the biology of the Mountain Chickadee (*Parus gambeli*) and its impacts on selected forest insects. In: J.G. Dickson, R.N. Conner, R.R. Fleet, J.C. Kroll, and J.A. Jackson, Eds. *The Role of Insectivorous Birds in Forest Ecosystems.* Pp. 217-260. Academic Press, New York NY.

Foelix, R.F. Biology of Spiders, 2nd Ed. Oxford University Press, New York. 330 pp.

Fowler, S.V. and M. Macgarvin. 1985. The impact of hairy wood ants, *Formica lugubris*, on the guild structure of herbivorous insects on birch, *Betual pubescens.* J. Animal Ecol. 54:847-855.

Fritz, R.S. and E.L. Simms 1992. *Plant Resistance to Herbivores and Pathogens.* University of Chicago Press, Chicago US.

Furniss, R.L. and V.M. Carolin. 1977. Western Forest Insects. U.S. Department of Agriculture Forest Service, Misc. Pub. No. 1399, Government Printing Office, Washington DC. 654 pp.

Gregg, R.E. 1963. *The Ants of Colorado.* University of Colorado Press, Boulder CO. 792 pp.

Grundel, R. and D.L. Dahlsten. 1990. The feeding ecology of mountain chickadees (*Parus gambeli*): patterns of arthropod prey delivery to nestling birds. Can. J. Zoo. 69: 1793-1804.

Gunnarsson, B. 1983. Winter mortality of spruce-living spiders: effects of spider interactions and bird predation. Oikos 40: 226-233.

Gunnarsson, B. and M.Hake. 1999. Bird predation affects canopy-living arthropods in city parks. Can. J. Zool. 77: 1419-1428.

Hairston, N.G., Smith, F.E. and Slobodkin, L.B. 1960. Community structure, population control, and competition. American Naturalist 94:421-25.

Hawksworth, F.G. and Wiens, D. 1996. *Dwarf Mistletoes: Biology, Pathology, And Systematics.* USDA Forest Service Agricultural Handbook 709. Washington DC.

Haemig, P.D. 1992. Competition between ants and birds in a Swedish forest. Oikos 65(3): 479-483.

Haemig, P.D. 1994. Effects of Ants on the Foraging of Birds in Spruce Trees. Oecologia 97(1): 35-40.

Haemig, P.D. 1996. Interference from ants alters foraging ecology of great tits. Behavioral Ecology and Sociobiology 38: 25-29.

Halaj, J., Ross, D.W. , and A.R. Moldenke. 1997. Negative effects of ant foraging on spiders in Douglas-fir canopies. Oecologia 109: 313-322.

Hogstad, O. 1984. Variation in numbers, territoriality and flock size of a Goldcrest *Regulus regulus* population in winter. Ibis 126: 296-306.

Holldobler, B. and E.O. Wilson. 1990. *The Ants*. Harvard University Press, Cambridge MA. 732 pp.

Howard, F.W. and A.D. Oliver. 1978. Arthropod populations in permanent pastures treated and untreated with mirex for red imported fire ant control. Environmental Entomology 7: 901-903.

Howe, H.F. and L.C. Westley. 1988. *Ecological Relationships of Plants and Animals*. Oxford University Press, New York US.

Johnson, D.E. 1998. *Applied Multivariate Methods for Data Analysis*. Duxbury Press, Pacific Grove, CA. 567 pp.

Kajak, A., Breymeyer, A., Petal, J., and E. Olechowicz. 1972. The influence of ants on meadow invertebrates. Ekol. Pol. 20: 163-171.

Mahdi, T. and J.B. Whittaker. 1993. Do birch trees (*Betula pendula*) grow better if foraged by wood ants? J. Animal Eco. 62:101-116.

Marquis, R.J. and C.J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology 75: 2007-2014.

Otvos, I.S. 1978. The effects of insectivorous bird activities in forest ecosystems: An evaluation. In: J.G. Dickson, R.N. Conner, R.R. Fleet, J.C. Kroll, and J.A. Jackson, Eds. *The Role of Insectivorous Birds in Forest Ecosystems*. Pp. 217-260. Academic Press, New York NY.

Petal, J. 1978. The role of ants in ecosystems. In: M.V. Brian, Ed. *Production Ecology of Ants and Termints*. Pp. 293-325. Cambridge University press, New York, NY.

Pravosudov, V.V., Pravosudova, E.V. and E.Y. Zimireva. 1996. The diet of nestling eurasian nuthatches. J. Field Ornithol. 67: 114-118.

Riechert, S.E. and A.V. Hedrick. 1990. Levels of predation and genetically based anti-predator behavior in the spider, *Agelenopsis aperta*. Animal Behaviour 40: 679-687.

Sih, A., Englund, G. and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology and Evolution 13: 350-355.

Skinner, G.J. and J.B. Whittaker. 1981. An experimental investigation of inter-relationships between the wood-ant (*Formica rufa*) and some tree-canopy herbivores. J. Animal Eco. 50:313-326.

Warrington, S. and J.B. Whittaker. 1985. An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*) I. Lepidoptera larvae. J. Applied Ecol. 22:775-785.

Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge UK. 328pp.

Zar, J.H. 1999. *Biostatistical Analysis 5th ed*. Prentice Hall, NJ

APPENDIX: Presented Abstracts

Mooney, K.A. 2001 University of Colorado, Boulder. Tri-trophic interactions and multiple predator effects in the canopies of ponderosa pine forests. Presented to the 86th Annual Meeting of the Ecological Society of America, Madison, WI, August 5-10.

Tri-trophic interactions between predators, herbivores, and plants can be modified by predator-predator interactions including intra-guild predation. I examined two separate tri-trophic interactions in the canopies of ponderosa pine forests. First, in 1999 I used whole-tree bird exclosures to document the effects of birds (A) directly on arthropod communities in ponderosa pine canopies, and (B) indirectly on pine foliage. To determine whether a second canopy predator, *Formica fusca*, affects patterns of avian predation I evaluated avian foraging patterns on control and ant-excluded trees in the 2000. Bird exclosure increased insect abundance by 44%, increased salticid spiders by 56% and increased ant abundance by 110%. Bird exclusion increased foliage herbivory from 4.7% to 7.3%. The presence of *F. fusca* did not affect avian foraging patterns. Bird exclosure increased herbivory despite the fact that intermediate predators (spiders and ants) were also more abundant. Second, in 1999 I used branch-level exclosures to document the direct effects of predation by pine canopy arthropods (A) directly on the lepidopteran herbivores of dwarf mistletoe (*Arceuthobium vaginatum*), a parasitic plant commonly found on pine, and (B) indirectly on dwarf mistletoe itself. Mortality of lepidopteran herbivores of dwarf mistletoe was 56% higher in the presence of their arthropod predators, but there was not a detectable indirect effect of predator manipulation on dwarf mistletoe biomass.

Mooney, K.A. 2001. Interaction between effects of birds and ants on ponderosa pine canopy arthropods. Presented to the 27th Annual Meeting of the Guild of Rocky Mountain Population Biologists, Abiquiu, NM Sept. 28-31, 2001

Both birds and ants have both been shown to individually have significat affect arthropod communities in forest canopies. Birds and ants have also been shown to interact with each other, both as competitors and as predator and prey. I will present some preliminary results from a factorial experiment in which I have excluded either birds, ants, or both from ponderosa pine canopies. The purpose of this experiment is to determine whether thecombined effects of bird and ants on the arthropod community of ponderosa pines differs from that predicted based on the individual effects of these two gropus of predators, i.e. whether there is significant interaction, in both a statistical and biological sense, between the two effects. I found the most significant effects of ants was to increase the abudance of Cinara spp. aphids. In the absence of ants, birds did not affect aphid abundance, but in the presence of ants aphid abundance increased approximately four-fold with the exclusion fo birds. This significant interaction suggests that the effect of birds and ants on canopy arthropod communities is largely dependent on the composition of the predator community.

Mooney, K.A., and Haloin,J. 2001. Effects of resource investment on *Eris aurantia* (Salticidae) nesting behavior following disturbance. Presented to the 27th Annual meeting of the Guild of Rocky Mountain Population Biologists, Abiquiu, NM, Sept. 28-31, 2001.

Salticid spiders, including *Eris aurantia*, build silken refuges from which they forage and within which they lay eggs. We predicted that the response of *E. aurantia* to a disturbance event that damaged this refuge would depend, in part, on the resources invested in that structure and that particular nesting sight. To test this, we destroyed the refuges of 30 spiders, noting the size of the refuge, the effort to displace the spider from this refuge, and whether the refuge contained eggs or spiderlings. We monitored the response of each spider for several weeks, noting whether or not they rebuilt their refuges in the same location, and if so the size of the rebuilt refuge and the duration of occupancy. We found that likelihood that *E. aurantia* rebuilds a refugia following disturbance was greatest when a refuge contained eggs, and lower when the refuge was either vacant or contained spiderlings.